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PERCEPTION AND MANAGEMENT OF CASSAVA (*MANIHOT ESCULENTA* CRANTZ) DIVERSITY AMONG MAKUSHI AMERINDIANS OF GUYANA (SOUTH AMERICA)

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ABSTRACT.—This article presents the ways in which Makushi subsistence economy and its farming practices, food preparations, cultural knowledge and social processes have all played a role in bringing cassava varietal and genetic diversity into existence. After comparing cassava varietal diversity among the Makushi of Guyana with that found in the rest of Amazonia, the authors discuss the genetic implications of traditional management and show that evolution in populations of domesticated cassava results from the combined action of natural and human selection. Various socio-cultural factors exercising selective pressure, in particular the exchange of planting material between farmers and the conceptual opposition of seedlings and plants coming from vegetative propagation, are examined. The approach adopted, which integrates indigenous botanical knowledge, elements of plant genetics and ecology, emphasises that diversity cannot be reduced to a finite stock of well defined, separate entities called varieties, but is, rather, a fluid and evolving process by which farm-grown varieties are continuously gained and lost.

Key words: Cassava, *Manihot esculenta*, Makushi Amerindians, Guyana, traditional agriculture

RESUMEN.—Este artículo presenta la manera en que la economia de subsistencia de los Malushi y las prácticas de cultivo, la preparación de las comidas, el conocimiento cultural y los mecanismos sociales han contribuído a una importante diversidád genética y varietal de la yuca. Después de un análisis comparativo de la diversidád de la yuca cultivada por los Makushi de Guyana con la que se encuentra en el resto de la Amazonia, el artículo discute sobre la simplicaciones genéticas de las prácticas de cultivo tradicionales, y muestra que que la evolución de las poblaciones de yuca cultivada es la consecuencia de la acción combinada

de la selección natural y la selección humana. Varios factores socio-culturales implicados en la selección, en particular los intercambios de estacas entre los cultivadores y la oposición conceptual entre la planta nacida de semilla y la planta obtenida por estaca són examinados. La integración de los conocimientos botánicos indígenos, de elementos de genética y de ecología muestra que la diversidád, lejos de estar reducida a un conjunto finito de entitades determinadas llamadas variedades, es al contrario un proceso fluido y dinámico, por el cual las variedades cultivadas son continuamente adquiridas y perdiddas.

RÉSUMÉ.—Cet article présente la façon dont l'économie de subsistance des Makushi ainsi que les pratiques de culture, la préparation des mets, les connaissances culturelles et les mécanismes sociaux ont tous contribué à une importante diversité variétale et génétique du manioc. Après une analyse comparative de la diversité variétale du manioc chez les Makushi de Guyana avec celle que l'on trouve dans le reste de l'Amazonie, l'article discute les implications génétiques des pratiques de culture traditionnelles et montre que l'évolution de populations de manioc domestiqué est la conséquence de l'action combinée de la sélection naturelle et la sélection humaine. Plusieurs facteurs socioculturels impliqués dans la sélection, en particulier les échanges de boutures entre les cultivateurs et l'opposition conceptuelle entre plante issue de graine et plante issue de multiplication végétative sont examinés. L'approche adoptée, qui intègre les connaissances botaniques indigènes, des éléments de génétique et d'écologie, souligne que la diversité, loin d'être réduite à un stock fini d'entités déterminées appelées variétés, est au contraire un processus fluide et dynamique par lequel les variétés cultivées sont continuellement acquises et perdues.

INTRODUCTION

While present concerns about the conservation of genetic resources have led to the reassessment of the human side of plant/people interactions, the questioning of the division between natural and artificial mechanisms of selection has prompted a growing number of researchers to pay particular attention to the ways in which people affect plant genetics (Salick 1995). These developments, which have given rise to a new type of economic botany that integrates ecological and evolutionary dimensions in the reinterpretation of plant domestication, cultivation and management, have resulted in renewed interest in traditional farming systems, known for maintaining high levels of biological diversity (Boster 1983; Salick and Merrick 1990; Salick 1992a; Brush et al. 1994). Traditional farming systems have so far been studied by geneticists, who have attempted to assess the level of genetic diversity found in collections of cultivated plants, including varieties, and by social scientists, who have carried out extensive ethnological surveys. However, only a few studies have tried to connect both genetic and ethnobiological aspects of the maintenance of varietal diversity (e.g., Quiros et al. 1990; Zimmerer 1991; Salick 1992b; Louette et al. 1997; Souza et al. 1997; Emperaire et al. 1998).

The overall objective of our investigation of cassava (*Manihot esculenta* Crantz, Euphorbiaceae) is to apply an integrative approach combining ethnological, ecological and genetic data in order to understand how the biological diversity of this cultivated plant is traditionally managed and maintained. For this, we have cho-

sen to study bitter cassava cultivation in a Makushi community of the North Rupununi savannas of Guyana, South America (Figure 1). Some of the results of our genetic studies are now available (Elias et al. in press); ecological studies are still in progress. The specific objective of this paper is to document the cultural knowledge and practices that have brought the genetic diversity of cassava into

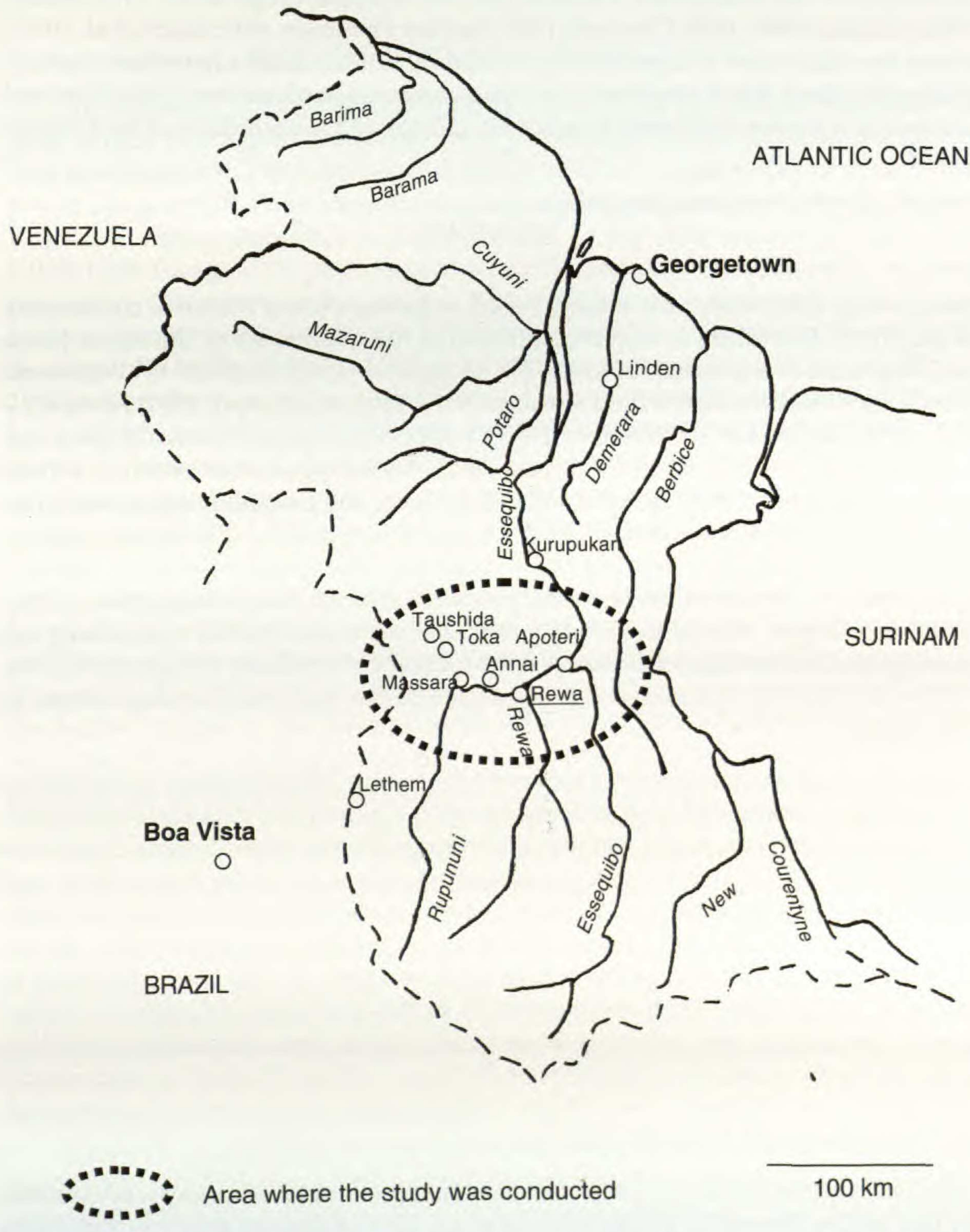

FIGURE 1.—Map of Guyana, showing the location of the Makushi communities where the study was conducted.

existence. This information on the cultural environment, combined with information on ecology, is essential to the interpretation of population genetics and evolutionary patterns (Elias et al. in press).

Bitter cassava, characterised by high cyanogenic-glucoside content of the tuberous roots, is the staple crop in the Amazon, where it has been cultivated for more than 3000 years (Renvoize 1972). Most cassava research to date has been conducted in the Northwest Amazon (see for example Hugh-Jones 1978; Boster 1984a; Dufour 1985, 1988; Chernela 1987; Van der Hammen 1992; Salick et al. 1997), where the cultivation and processing of (mainly bitter) cassava have been meticulously described. Rival (in press) presents a comparison of cassava cultivation and processing between northwest Amazonian groups and Amerindians of the Guyana shield.

METHODS

Site of study.–Our study was mainly based in Rewa, a small Makushi community of the North Rupununi in Guyana, situated at the confluence of the rivers Rewa and Rupununi (forest area), 50 km WSW of Apoteri (4°02′ N, 58°35′ W). Marianne Elias spent 9 months over 3 field sessions in the Rupununi (April 1997, February – May 1998, September – December 1998); Laura Rival spent 5 weeks (2 field sessions in April 1997 and April 1998); and Doyle McKey spent one month (one field session in October 1998). In April 1998, there were 162 people living in Rewa (including three Wapishana men, six Wapishana women, and two Patamona women), forming 27 households. Because of its small size and relative isolation, Rewa is less subject to commercial and political pressures than savanna communities. Other Makushi villages, located in the savannah area, were also visited. Concerning the farming system, no major differences were found between these villages and Rewa, which can thus be considered representative of the Makushi farming system in this region.

Collection of ethnographical data.–Our methods involved observations, participation in farming practices and food processing, open discussions, structured and semi-structured interviews and questionnaires. Symbolic and other cultural data were collected as part of a participatory research programme led by Laura Rival and involving the close collaboration of two remunerated Makushi women researchers. We tried to work with as many farmers as possible; however, three female farmers (ages: 22, 35, 52) and two male farmers (ages: 41, 50) were identified as our main informants. As almost everybody in Rewa is fluent in English or Portuguese; discussions and interview were conducted in these languages, including some Makushi words for critical points. Bilingual villagers helped us with people who spoke only Makushi. One villager in Rewa and two villagers in the savannah area helped us with Makushi spelling.

Assessment of varietal diversity and of its distribution.–Varietal diversity was assessed by first asking farmers to bring leaves of every kind of cassava they cultivate, then by visiting farms and interviewing farmers. To estimate the equitability of diversity distribution among cassava farmers we used the index of equitability, which

is often applied to estimate the "evenness" component of the diversity of biological assemblages.

It is calculated as follows : $E = \frac{\sum_i p_i . \ln p_i}{\ln S}$, where $p_i = \frac{n_i}{S}$, $S = \sum_i n_i$, and n_i are the numbers of households that cultivate variety *i* (respectively, the number of varieties owned by household *i*).

MAKUSHI CASSAVA FARMING TODAY

The Makushi, a Carib-speaking group, live in the Rio Branco-Rupununi region, which is a region politically divided between Brazil (Roraima State) and Guyana (Region 9). There are approximately 20,000 Makushi today, of whom 7,000 live in Guyana (CIR 1993). Historical records of Makushi presence in the Rio Branco-Rupununi region date back to the early part of the 18th century (Rivière 1963; CIDR 1989; Farage 1991; Hemming 1994, 1995; Santilli 1994). With cattle ranching expanding at the turn of the century, they experienced increased land shortages and pressure to work as domestic servants or cowboys, and many of them left the Roraima hills in Brazil for the Rupununi savannas of what is now Guyana (Farage 1991), where they can still be found, living in relatively small communities, headed by a captain or "toushau." Makushi families historically traded manufactured goods for cassava and cassava derivatives, particularly farine, a meal made of dried granules of grated cassava (Farabee 1924; Diniz 1966; Farage 1991). White settlers needed the Makushi as much for their agricultural products as they did for their labour force, and there is little doubt that such demands modified the indigenous agricultural system. Such influence accentuated the importance of horticulture over hunting and gathering, and reinforced the tendency towards sedentarisation in nucleated villages. If, like many other Amerindian groups, the Makushi had traditionally produced cassava surpluses to prepare fermented drinks for festive occasions, the condemnation of such politico-ritual activities by missionaries, the new trade opportunities, and additional factors linked to interethnic contacts, led to the utilisation of cassava surpluses to make farine for sale, a trend which has influenced the choice of cultivated varieties.

Bitter cassava cultivation is central to Guyanese Makushi slash-and-burn agriculture, which is still directed toward subsistence, rather than market, production. Many varieties of bitter cassava are maintained (Makushi Research Unit 1996), and the diet is supplemented by other starchy crops such as yams (*Dioscorea* spp.), corn (*Zea mays* L.), sweet potato (*Ipomoea batatas* (L.) Lam), sweet cassava (*Manihot esculenta*), plantains (*Musa paradisiaca* L.), or vegetables such as pumpkin (*Cucurbita maxima* Duch. ex Lam.), shallots (*Allium cepa* 'aggregatum' L.) and onions (*Allium cepa* 'cepa' L.), or fruits such as watermelon (*Citrullus lanatus* [Thunb.] Mansf.), as well as fish and meat (game and cattle).

Agricultural activities are conditioned by climatic and edaphic factors. Wet (from May to September) and dry (from November to March) seasons are pronounced and interspersed with brief transitional periods. Two factors make savannah soils particularly unsuitable for crop cultivation. In addition to being particularly infertile, they are subjected to weather extremes; they are almost en-

tirely flooded during the rainy season, and parched under a scorching sun during the dry season. This explains why people traditionally lived in forest galleries along main rivers, where soils remain moist throughout the year, and used the savannah mainly for seasonal hunting.

With the rare exception of plantain and cotton farms, Makushi farms are, on the whole, bitter cassava farms. Sweet cassava, yams, sweet potatoes, plantains, pumpkin or watermelon are sometimes inter-cropped with bitter cassava, but these crops are rather marginal. Bitter cassava is consumed daily as farine (***u'wi***), cassava bread (***kai***), fermented drinks (***parakîrî, kasiri*** and ***wo'***), casereep (***kumasi***), a black, thick paste used throughout Guyana to cook meat and fish, and, finally, starch tapioca (***imu yanasa***) or porridge (Figure 2).

Each year during the dry season, households clear new farms (ranging from 400 m_ to more than one hectare) in old fallows or secondary forest, that is, on land that has already been used in the past to cultivate cassava. As the main problem in farm management is protection of crops from predators and fluctuating climate, risk aversion, particularly the risk of flooding and of leaf-cutter ant invasion, seems to play a greater role than soil fertility in the choice of farm sites.

Clearing a new farm (***mîî ya'tî***) is considered hard work, and is exclusively a male activity. It was traditionally performed by a man with the help of his relatives and friends (***mayu***), in exchange for food or drinks (***parakîrî*** or ***wo'***). Cooperation in forest clearing now tends to be restricted to immediate kin, for example, father and son. New farms are burnt (***mîî po'tî***) in March or April, just before the first rains. Fire is propagated with lit kokerite (*Attalea regia* [Anderson]) fronds, a process difficult to control and which may lead to forest fires and crop

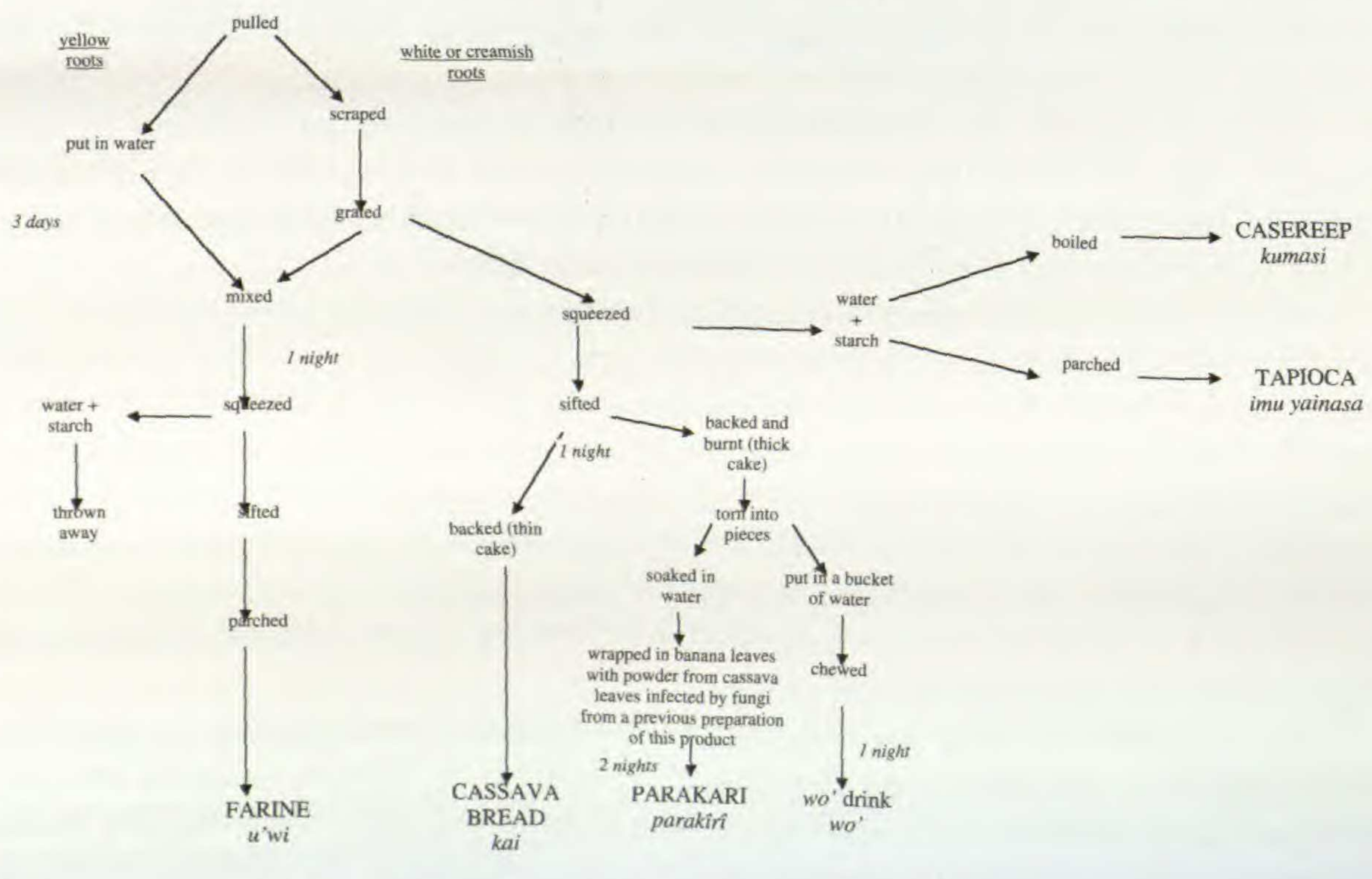

FIGURE 2.—Processing and products made of cassava by Makushi Amerindians.

losses when weather conditions are particularly dry. Ground cleaning (***mîî kui ma***), the third stage in preparing a new cassava farm, is undertaken by the entire household, children included. The male farmer hoes (***ya nu mîî***) the field, and shapes the soil into mounds (locally known as "banks"), in which cuttings (locally called "cassava sticks", ***kîsera*** in Makushi) are planted (soil mounding, a practice rather uncommon in Amazonia, is also found in the Upper Xingu [Carneiro 1961]).

Female farmers, sometimes accompanied by their children, divide the long stems of freshly harvested cassava into cuttings. Although they store long stems in shady places or keep them for weeks, slightly buried in the ground before using them as planting material, farmers prefer to prepare cuttings directly from a living plant. Moreover, the selection of cuttings depends on whether a plant is healthy and whether it has produced a generous harvest of roots. Cutting the stems is a woman's work, but planting is usually done by men, although this is not always the case in other villages (Mary Riley, University of Illinois at Chicago, USA, personal communication). Three to five cuttings of the same variety are planted together in each mound, pointing to the west. Although most people are aware that cuttings planted eastward grow as well as those pointing westward, they still maintain that a westward orientation protects the plant from the sun and favours its growth. There may be a connection between this belief and the common Makushi practice of burying corpses with the feet pointing east, head west, and the face looking to the rising sun (data collected by Laura Rival in Massara, April 1997). Another common practice observed by Laura Rival in the field, and aimed at encouraging growth and tuber production, is to plant a magical plant (generically known as ***bina*** in Guyana) in the middle of the field, or to chew the root of such a plant, and spit it over the mounds (see also Makushi Research Unit 1996).

The time it takes a farmer to plant a new cassava farm depends on his availability, and on how many stems the household has in stock; it thus varies greatly from farm to farm, and from individual to individual. Some farmers plant cassava every day for a week, and then stop for two or three weeks before continuing. As a result, several months can separate the youngest and the oldest plants in a single farm. This practice, as well as the planting of varieties with different maturation rates, ensures a constant supply of harvestable roots throughout the year. Cassava roots are harvested on average nine months after planting (range: 4 months to 2 years), and the crop requires little care during this period. A first crop does not generally require weeding more than three times, but women may perform spot weeding every time they harvest roots (both weeding and harvesting are female tasks).

Roots are harvested when and as they are needed. Stems of freshly harvested cassava are sometimes replanted in mounds hoed again for what the Makushi call the "second crop." More commonly, they are taken to a new farm, where the best cuttings are selected and planted. The surplus is stored, hidden under kokerite fronds, or planted in tight bundles at the edge of the farm. Some may be given to neighbours, relatives or friends. Unused stems stored in bundles also grow and, if the weather is not too dry, develop tuberous roots nine months after. These roots are harvested, but the stems are usually discarded, being used as planting material only if the farmer is desperately short of cuttings.

After harvest, first crop farms are planted with a second crop of cassava. Second crop farms require greater weeding efforts, and their productivity is lesser. When harvested, they are not generally hoed again and replanted, except if the parcel cleared for the first crop is located in primary rainforest or old secondary forest, where the rich, deep forest soil allows for a third, and even sometimes a fourth crop. Abandoned farms are soon covered with fast growing pioneer vegetation. Old farms are left fallow for two to twenty years, or more. Although farm land is not privately owned, old fallows are customarily left for the use of the families who first cultivated them.

As in most Amazonian societies, cassava processing is the responsibility of women, and food intimately connected with gender specialisation. However, it is not uncommon to see a man helping his wife making edible products out of bitter cassava, which contains a high concentration of cyanogenic glucosides and must be detoxified before consumption. Roots are scraped, and the skin and inner peel (except in the preparation of ***parakîrî*** and ***wo'***) removed. They are then washed and grated. The grated pulp is squeezed in the long plaited cassava sleeve press, known in Guyana as matapi (***tinki***). To make farine, women first mix fresh grated cassava with roots that have fermented for three days, and then squeeze the mixture. The half-dry pulp is then used for preparing the final products (Figure 2). This process ensures that most of cyanide is removed (Dufour 1989, 1995)

To sum up, the farming system so far described is broadly similar to those found among other Amazonian bitter cassava farmers (see in particular Dole 1963, 1978; Yde 1965; Diniz 1966; Grenand and Haxaire 1977; Hugh-Jones 1978, 1979; Carneiro 1983; Dufour 1983; Chernela 1987; Mowat 1989; Van der Hammen 1992; Grenand 1993; Emperaire et al. 1998). We are fully aware that the farming system we have studied may be a recent development linked to sedentarisation. We suspect, for instance, that the present shortage of farmland has resulted in sharp reduction of fallow periods. This shortage, dramatic in the savannah, where farmers have to walk for hours or paddle for several days to reach their farms, is beginning to affect Rewa as well. Another consequence of sedentarisation is that farms must last longer, so people tend to select varieties that can stay in the ground longer, such as, for example, the popular "white man stick" that remains harvestable two years after planting.

CASSAVA DIVERSITY AND ITS PERCEPTION BY THE MAKUSHI

Cassava diversity in one Makushi village.– Cassava varieties are distributed in farms either in a structured pattern (i.e. planted in contiguous monovarietal patches), or at random, the latter distribution being more frequent. Every variety has a Makushi name, of which the English translation is usually known. In Rewa, we collected 86 different names of cassava varieties (Table 1), corresponding to 76 varieties (while some varieties were given different names by different farmers, some farmers knew several varieties under a single name). Varieties that farmers were unable to name were not included in the survey. Each household owns on average 16 varieties (Table 1). Varieties differ in their frequency of representation among households. While some are shared by almost all farmers (for example, ***paranakîrî pîye*** and

kuraatuma pîye), others are owned by only a few, or even by a single person (for example, ***oronkî pîye*** and ***dominko ye***). The equitability index for cassava varieties is 0.63 (it would be equal to 1 if all varieties had the same frequency in the village), and 0.52 for households (it would be equal to 1 if all the households had the same number of varieties). No one in Rewa has an accurate or exhaustive knowledge of the varietal diversity present in the village.

Sweet cassava is planted either in the farm, together with bitter varieties (but the two types of roots are not mixed, as sweet cassava is not cultivated for the same purpose), or in the kitchen garden next to the house. Farmers say that sweet cassava roots develop more slowly than bitter ones, and that the plant grows taller. Four different types of sweet cassava, all called ***kana*** as opposed to ***kîse*** (bitter cassava), are grown in Rewa. They all have white roots, and are generically referred to with English names ("brown stick," "four months," "eighteen months," or "white stick"). The lack of a proper Makushi name confirms that sweet cassava is not regarded as "real" cassava; like yam or sweet potatoes, its place in Makushi diet is secondary (Makushi Research Unit 1996). Semi-quantitative tests based on a colorimetric method using alkaline picrate (Williams and Edwards 1980) confirmed that all varieties designed as bitter by the Makushi have a high cyanide content, whereas so-called sweet varieties have a low cyanide content (Elias unpublished data, see also Dufour 1988).

Perception of bitter cassava diversity.– Makushi lore includes several myths referring to cassava and its origin, as well as to Cassava Mother (***kîsera yan***), the master spirit that owns the plant, looks after its well being, and ensures good harvests (Rival in press). Although myths are complex cultural representations that cannot be reduced to one single dimension or message, Makushi myths relating to cassava clearly convey the idea that this plant exists first and foremost as a cultivated, that is, a domesticated or cultural plant, whose inalterable blueprint is the master spirit Cassava Mother, and whose origin relates to the transformation of a human body. Wild cassava[1] is represented as a degenerated cultivar escaped from gardens, which has stopped producing tuberous roots, because it now grows in non-cultivated (i.e. non-cultural) spaces, such as hill tops in the savannah.

Taxonomy.–Savanna-dwelling farmers of mixed origin (i.e. of Makushi and Black, locally known as "dougler"), and Makushi who have no direct knowledge of cassava cultivation, recognise only three kinds of cassava: yellow, cream and white varieties. They differentiate them by color and use, as cassava bread is made with the roots of white varieties, and farine with the roots of yellow varieties. The first morphological trait mentioned by a farmer is the color of the root, and its intensity. Three main categories are actually differentiated: yellow types, creamy types (which non-farmers confuse with yellow types), and white types. This classification, also found among other groups (Emperaire et al. 1998), plays a determinant role in evolutionary terms. This may explain why Makushi people tend to underestimate their varietal diversity, and why outsiders are only aware of differences in root color.

Named varieties constitute the second, and more ambiguous, level of classification. Varieties are named after animals, plants, objects, dishes, qualities, and

TABLE 1.—Cassava varieties found in Rewa, and their distribution among 24 families.

Makushi names	English names	AM	NE	WE	VA	DP	JM	TA	RE	JE	MA	AE	DH	FW	JA	CS	EK	NI	WA	JH	PH	CH	LE	ZP	HS
ainis pîye	Inez stick				x										x										x
aknes pîye	agnes stick					x																			
akuriu ye	agouti stick					x			x										x			x			
amilton ye	Hamilton stick			x																					
amo'ko pîye =	grand father st. =																								
danal pîye	Danal stick	x				x			x		x									x					
amuru pîye	thick stick		x		x													x	x					x	x
ankela pîye	Angela stick																					x			
anra pîye	crane stick	x	x		x	x			x		x		x	x		x		x	x		x	x	x		x
dominko ye	Domingo stick																					x			
eti pîye	Eddie stick				x	x							x				x		x		x	x			x
eni pîye	Eni stick				x																				
esekwipo ye	Essequibo st.				x															x		x			
isman pîye =	Isman stick =																								
sandra pîye =	Sandra stick =																								
amuru pîye ?	thick stick ?				x	x			x						x	x			x		x		x		
kaima pîye =	pumpkin stick =																								
eri pîye	Ely stick	x	x		x	x	x	x		x	x		x	x			x		x	x			x		x
kanaima ye	jombie stick				x						x														x
karmani pîye	Carmani stick						x																		
kasiri pîye	kashiri stick		x										x										x		x
kediam pîye	Kediam stick							x																	
kini' pîye (2 types) =	dry stick =																								
reni pîye	Reni stick	x	x		x	x		x	x	x	x		x	x		x	x	x	x			x	x		x
ko'ko pîye	grand mother stick																					x			
kraiwa pîye	brazilian stick		x			x	x				x			x	x				x		x				x
kari'na pîye	Carib stick				x																	x			
kompani pîye	company stick									x															
krompî pîye	?					x																			
kumia ye	fish stick																					x			

Table 1 (continued)

Makushi names	English names	AM	NE	WE	VA	DP	JM	TA	RE	JE	MA	AE	DH	FW	JA	CS	EK	NI	WA	JH	PH	CH	LE	ZP	HS
kunani pîye	fish poison st.					x							x												x
kuraatuma pîye (2 types)	caiman stick	x	x	x	x	x	x	x		x	x		x	x	x	x	x	x	x	x		x	x	x	x
kurarî pîye	curral stick	x	x		x			x		x	x			x			x			x	x	x	x		
kuraswa pîye = ***selia pîye =*** ***waimko pîye***	Crash Water st = Celia stick = Waimko st.	x	x			x		x		x	x		x		x				x		x		x		x
lio pîye	Lio stick																		x						x
mai pîye	bitter stick	x						x		x			x						x				x		
maka pîye	maggah stick									x															
makarpon ye	Makar pond stick																			x					
marasî pîye	marudi stick				x			x			x								x						
mauri pîye	Mauri stick								x			x												x	
meekoro pîye	black man stick		x		x		x				x	x	x	x		x		x							
mepriko ye	Elfrida stick					x										x				x					
omano pîye	Omano stick																					x			
oronkî pîye	bamboo stick						x																		
paapa ye	father stick						x	x		x															
pakaima ye	buffalo stick							x			x														
pali pîye = ***kaiwan pîye***	Bali stick = fat boy st		x	x	x			x			x		x					x	x					x	x
papîro ye	Pablo stick	x			x			x		x			x		x		x						x		x
parakîrî pîye	parakari stick		x							x									x		x				
paranakîrî pîye	white man stick	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
paranakîrî pîye ***itakon ye =*** ***naman pîye***	white man stick cousin = Naman stick		x		x					x	x							x	x		x		x		x
paranakîrî pîye ***perurupe***	white man stick seedling				x																				x
pinkîu ye	peccarie stick					x	x				x			x		x							x		x
pîraun pîye	Brown stick																					x			
pîrikwa pîye = ***ipo ye***	bird stick = sweet stick	x	x		x	x		x		x	x		x	x		x		x				x	x		x

Makushi names	English names	AM	NE	WE	VA	DP	JM	TA	RE	JE	MA	AE	DH	FW	JA	CS	EK	NI	WA	JH	PH	CH	LE	ZP	HS
pîrori pîye	Pearl stick					x																			
prona pîye	brown stick				x						x														
rekî pîye	thick stick																								x
rikîtun pîye	black stick			x																					
rora pîye	green stick	x						x			x														
sakari pîye	Zaccharie stick							x																	
saketa pîye	Sagda stick																					x			
saprî pîye	fine fish stick	x						x		x	x				x										
seruak pîye	3 months stick						x									x									
siya pîye	Shea stick		x					x		x	x			x			x		x						x
siment pîye	cement stick		x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x		x		x
siwal pîye	Sea Wall stick					x													x						
sona pîye	Jona stick		x		x						x														
supra pîye	cutlass stick		x		x			x		x	x	x	x	x		x	x				x	x	x		x
tare'kîya pîmoi pîye = suyu ye = five month stick = u'wi pîye ?	water turtlle egg stick = yellow stick = 5 months st = farine stick ?				x	x	x	x			x			x					x	x		x			x
tari ye	black potatoes stick																								x
tikîri pîye	?									x			x												
toni pîye	Tony stick												x												
urakasa ye	pigeon stick										x														x
usariu ye	deer stick					x																			
u'wi pîye	farine stick		x		x	x	x		x		x	x	x	x	x		x		x						
uyara pîye	macaw stick (cassava heart)									x														x	
waakîri pîye	I love stick		x																						
walakîse pîye	Walax stick												x												
wo' ye	drink stick	x	x	x	x														x	x					x
total number of varieties : 76		14	22	7	28	22	12	21	9	20	27	6	20	15	10	12	11	10	23	11	11	19	16	7	27

Table 1 (continued).

according to the place of origin or the person from whom cuttings were obtained. Names derived from animals, plants, objects, dishes, and qualities are said to be more authentic and traditional than those based on Christian names and toponyms, with which they often overlap. For instance, the real name of "Ely stick" is "pumpkin stick," but as the farmer who received it from Mrs. Ely had forgotten the real name, she chose to call the new variety after Mrs. Ely. Almost all the inhabitants of Rewa speak both Makushi and English, but bilingualism does not seem to affect the naming system, given that all Makushi names have an English translation. We were told that it is the husband's, rather than the wife's, responsibility to give names to new varieties. On the whole, the Makushi naming system is similar to those used by many other traditional Amazonian groups (Salick et al. 1997; Emperaire et al. 1998).

Visits to various farms with different informants allowed us to confirm that farmers use the taxonomic classification outlined above fairly consistently. Eight times out of ten, they agree on what name to give to a particular variety. However, since the varietal make-up of each farm is different, a farmer visiting a neighbour's farm may be unable to name some of the varieties. We also detected several cases of synonymy and of homonymy (Table 1). The first genetic analyses, which are the best tools to detect such events, have confirmed these observations (Elias et al. in press).

Accuracy of taxonomy is of great importance in determining evolutionary pressures on cassava, since individual human selection acts on taxonomic units, locally identified as varieties. The fact that generic terms are increasingly used (at least in our informants' perception) may lead to an impoverishment of the highly specific variety vocabulary. For example, a really yellow variety is now commonly referred to by the generic term "farine stick" and a variety hard to grate by the term "dry stick", while an increasing number of varieties are called by the names of those from whom they were obtained. As a result, a farmer may have two or three types of "farine stick," "dry stick," or "Bali stick". However, most farmers can still differentiate among homonymous varieties. They can, for example, distinguish the "dry stick" with broad leaves from the "dry stick" with narrow leaves, and explain these differences accurately to the botanist. But we are not entirely certain that they are able to distinguish two morphologically close varieties with exactly the same properties, or coming from the same place, if they call them by the same name. The consequences of such taxonomic impoverishment are discussed below.

Recognition process.–The Makushi seem to identify their varieties all at once, just as they or we identify people we know. Several farmers told us that they cannot name a variety before checking the appearance and quality of the roots. This instantaneous and integrative recognition process, which appears to depend entirely on the plant phenotype, was first identified by Shigeta (1996), who calls it "face-to-face recognition."

Our hypothesis is that the recognition process operates on the basis of an unconscious hierarchisation of salient characters. This is best illustrated when a plant is hard to identify, because of phenotypic plasticity. The overall aspect of the stem is the first character observed, and the most important for defining the identity of

the plant. The next salient traits are, in decreasing order of importance, the aspect of the leaves, the color of the petiole, the external aspect and color of the root, and, finally, the flowers. These observations are concordant with those of Boster (1985) and of Emperaire et al. (1998).

While certain varieties are preferred for particular uses, there is much functional redundancy among varieties, and there appears to be no practical reason for having so many varieties of bitter cassava. The Makushi seem to enjoy diversity for its own sake, and more for aesthetic and recreational reasons, or out of scientific curiosity, than for security purposes. Our observations corroborate those of Carneiro (1983), who noted that the Kuikuru (Brazil) cannot explain why they have so many varieties; they just have them. Makushi farmers also say that they do not know, that they simply like seeing many different types of cassava in their farms. Like collectors, they seek to cultivate as many varieties as possible. They are driven by a deep-seated curiosity that pushes them to acquire new types continuously, "to try them out." This readiness to experiment has real implications for the structure and dynamics of cassava diversity.

THE DYNAMICS OF DIVERSITY

Cassava diversity is not static, and farmers experience intentional or unintentional losses of varieties, for which they compensate by acquiring new types. As stated before, acquiring new types can also be motivated simply by curiosity. We review here environmental and human selective factors involved in the dynamics of diversity.

Environmental selective factors.–Severe droughts and floods are recurring climatic conditions which can lead to the loss of varieties, and to which Makushi people have learned to adapt. According to our informants and our own observations, exceptionally dry weather such as that caused by El Niño from August 1997 to April 1998 kills recently planted and growing cassava alike. Drought affects root production, and can destroy all the propagation material. Varieties present in low densities, or owned by a few farmers only, are more likely to disappear. The Makushi have therefore developed special planting strategies to protect the cuttings from drought, and, to a lesser extent, flood. Farmers, for example, are careful to keep in the soil cuttings which, at first sight, look dried-out but which will almost certainly sprout again with the first showers. Mounds are reshaped with taller profiles, and replanted with six or eight (instead of four) cuttings to maximise the chances of having at least two well-developing plants in each. The general strategy is to prioritise the long-term reproductive cycle. Rather than saving harvestable roots, farmers try to preserve the stems as "germplasm banks". For this, they look for swampy areas, which are under normal circumstances flooded, and transport their best stems -sometimes over great distances- from their farms to the swamps, to stock them in large bunches there until it rains (Rival 1998).

Whereas cassava varieties in many parts of South America and Africa are seriously affected by diseases (cassava bacterial blight, Boher and Verdier 1995; African cassava mosaic virus, Fauquet and Fargette 1990), varieties in Rewa do not seem to suffer much from disease. However, in 1998, a new plague locally called "white

disease" (***turere***) caused by a small white insect (*Aonidomytilus albus*, Hemiptera: Diaspididae) which kills all affected plants struck all the high forest farms located three hours downriver from the village. One family with downriver farms lost all its cassava varieties.

Farmers seem to have many problems with, and often complain about, herbivores (Table 2). Leaf-cutter ants *Atta* spp. ("acoushi ants", ***kuinan***), which often destroy entire farms, and are very difficult to get rid of, are identified by farmers as the most dangerous predator of cassava. Farmers may decide to abandon a farm altogether, rather than try to eliminate ants. Other herbivores feeding on leaves usually act sporadically, and rarely kill plants. But their predatory activities may nevertheless dramatically affect plant vigour and root production, even causing roots to become watery. Plants that are frequently attacked by herbivores may not be multiplied. The "carelessness" of peccaries and tapirs, which often trample and destroy everything when feeding in a farm, may also lead to variety loss. Farmers do not seem to be aware of any particular herbivore/variety association, and information collected from different farmers regarding perception of varietal resistance was contradictory, which could reflect either strong soil/genotype interaction for resistance, great variability, or lack of interest in this feature.

Human selection.–As a cultivated crop, cassava is under intense human selective pressure. Vegetative propagation allows for the instantaneous selection of phenotypes of interest. Farmers, who can decide whether or not to keep a variety, to a certain extent also control the relative frequency of each variety. If there is no conscious selection for resistance to pests, diseases, or climatic conditions, some varieties will nevertheless be multiplied, whereas others will decrease in frequency. As far as we were able to observe, there is no directional selection on maturity rate either, since farmers need both precocious and late-bearing varieties in order to minimise risk and secure a continuous supply of harvestable roots. As scientists, we were even asked jokingly to invent a new and improved variety that would have such a broad maturity rate spectrum that there would be no need to grow any other variety.

TABLE 2.—Main wild herbivores feeding on cassava in Rewa.

class of herbivore	species	Makushi name	attacked parts	importance of damage
Insects	*Atta* spp. (leaf-cutter ants)	***kuinan***	leaves	+++
	Erinnyis ello (larvae of a sphinx moth)	***arari***	leaves	++
Birds	unidentified	***anakwa***	leaves	+
Mammals	*Mazama americana* (brocket deer)	***usari***	leaves	+
	Dasyprocta agouti (red rumped agouti)	***akuri***	roots	+
	Dasyprocta prymnolopha (black rumped agouti)	***akuri***	roots	+
	Agouti paca (paca)	***urana***	roots	+
	Tayassu pecari (white-lipped peccary)	***pinkî***	roots	+++
	Tayassu tajacu (collared peccary)	***pîraka***	roots	+++
	Tapirus terrestris (tapir)	***waira***	roots	+++

Taking up Boster's (1984a) hypothesis, McKey and Beckerman (1993) suggest that the productivity criteria include many other agronomic features. Human selection for productivity would combine with natural selection for survival and resistance. Like other Amazonian cassava cultivators (Boster 1985; Chernela 1987; Salick et al. 1997; Emperaire et al. 1998), the Makushi consciously select varieties primarily for their productivity. For instance, every household in Rewa has the ***paranakîrî pîye*** ("white man stick") variety, which produces high yields. It is the most frequent variety in 17 of the 24 farms included in our census. Yield is, however, highly variable among farmers and crops. Some varieties can be very productive in the first crop, but do poorly in the second, whereas others, which do not have a very high production in the first crop, do well in the second.

The color of the root is another important criterion for selection. The main dish in traditional Makushi diet is cassava bread made with white varieties. But when ranchers settled in the Rupununi in the 1930s, demand for farine, a staple with which they fed their workers, soared. Farmers responded to the demand by preparing increasing quantities of farine, which is made with yellow varieties, and they also increased the proportion of farine in their own diet, thus multiplying yellow varieties at the expense of white ones. This shift from cassava bread to farine, and from white to yellow varieties, is widely recognised as a recent phenomenon (see in particular Yde 1965). People nevertheless say that they like farine, which is easy to store and process, and that they want yellow forms, hence their eagerness to acquire yellow varieties. Four "really yellow" varieties are found locally, of which at least one is cultivated in great quantities.

Varieties are also selected for their culinary or "processability" properties, but these criteria vary greatly from farmer to farmer. Some women we interviewed prefer watery roots, which are easier to grate, whereas others liked dry roots, richer in starch. Aesthetics also play a role in selection, and a variety with an unusual combination of morphological characters undeniably arouses the farmer's curiosity and interest.

In addition to selecting varieties according to these criteria, farmers also protect rare varieties, thus encouraging frequency-dependent selection. A variety is rarely discarded, even if it is not very productive. Low-yielding, rare varieties are simply kept at low density (i.e. one or two mounds per farm), and this is considered enough to prevent their loss. Farmers explain that they do not like losing varieties, for a "bad" variety sometimes becomes "good" under different conditions. Rare varieties, however, become more vulnerable to loss by direct or natural selection. Finally, farmers lose varieties, not only because of environmental pressures or deliberate choice, but also because of bad space management. As each farm is limited in size and contains a finite number of mounds, there is sometimes no place left for experimental planting, and cuttings of marginal varieties may no longer be available when space becomes available again. If this occurs, the farmer has lost this variety. In sum, conscious human selection on cassava varieties is rather lax; it acts primarily to preserve diversity, rather than to maintain or augment some particular desired traits.

The exchange of cuttings and the management of volunteer plants grown from seedlings, which represent two means of acquiring new varieties or recovering lost ones, greatly contribute to the maintenance of cassava diversity.

Exchange networks. Farmers can recall the origin of all the varieties they have in their farms, no matter how far back they have to go. In former times, when the rule of uxorilocality and bride service was more generally applied, a young husband was expected to cultivate with his wife the farm of his parents-in-law, until his father-in-law gave him the permission to set up his own farm. The young husband would then receive a share of cuttings from his father-in-law, a stock which he complemented with cuttings brought from the farm of his own parents. The young wife would receive cuttings from her mother, sisters, mother-in-law and sisters-in law. The couples we interviewed always specified which varieties were brought into the conjugal farm by the husband, and which by the wife.

It is perhaps because a transfer of cuttings is initiated by request from a farmer in need that farmers so accurately remember the origin of the cuttings they cultivate. The most general term used to express the idea of transfer is "borrowing." A farmer short of planting material or willing to try a new variety asks another farmer for stems, which he or she will "repay" at a later stage with stems of a different variety, or with farine or ***parakîrî*** made with roots from the borrowed varieties. Delayed reciprocity has been observed among other Amerindian groups, such as the Aguaruna (Boster 1986). There is no specified rule on how long after having "borrowed" a farmer must "give back." The only time when transfers are not receiver-initiated, and when there is no pay back, is when a farmer donates cuttings to compensate damages, such as the destruction of part of a neighbour's crops through uncontrolled fire. The exchange of cuttings between closely related kin and neighbours whose farms are contiguous and who still practice a form of shared labour (***mayu***) is less formal and generalised, in the sense that strict reciprocity is not an issue. Only very occasionally will a farmer acquire cuttings of a rare variety by paying with cash, a cutlass, a bicycle or any other trade item. This type of exchange is more likely to occur between unrelated farmers who do not live, and have no family connection, in the village.

Two types of exchanges, one "massive" and the other "occasional," can be distinguished. Farmers who need large amounts of planting material for a new farm borrow cuttings from just a few varieties, which they usually already possess, but not in sufficient quantity. Those who want to try out a variety they do not have in their farm ask for a stem or two while visiting neighbours, friends or relatives. Farmers, who are always keen to acquire new varieties, carefully multiply the trial cuttings until reaching the desired density. The closer the locality from which a new variety originates, the more likely the retention of its real name will be. In contrast, a variety coming from a distant locality may be called after a toponym, for example "Shea stick" or "Crash Water stick."

In contrast with Chernela (1987), who has reported exchanges over an area 465 km wide, most Makushi cutting exchanges (and all massive exchanges) occur within the village community, in particular among immediate neighbours, who are usually related through descent and marriage (unpublished data). As a result, some families never interact, while others are continuously exchanging cuttings. Frequent exchanges between the same families are expected to lead to taxonomic homogenisation (Boster 1986). According to informants, cuttings were not traded across ethnic boundaries in the past, and even inter-village exchanges were -and still are- restricted, which, of course, does not exclude acquisition through war-

fare, looting, and the taking over of another tribe's old farms. Some farmers carefully avoid asking for cuttings, as they derive great prestige from relying on their own stocks, while lavishingly giving away to borrowers. Others, who keep their farms at a distance, never invite visitors, and share only reluctantly, are considered "stingy." Yet others do not dare asking for coveted cuttings, which they surreptitiously pick from the farms of neighbours or hosts (a behaviour which may lead to generalised theft in times of drought and starvation). To summarize, while some families always experience a deficit of planting material, others almost never borrow cuttings. And whereas some share their surpluses generously, others prefer to let their unused bundles of cuttings dry out. When examining the social networks underlying massive exchanges, we soon identified "source" families, whose efficient management of cassava production not only prevented them from experiencing shortages, but also ensured that they usually disposed of sufficient planting material to give away. "Sink" families, in contrast, managed their stocks poorly, often ran out of cuttings for their new farms, and heavily depended on borrowing. "Source" farmers are proud and respected community members, with a higher status than "sink" farmers.

Tepuru pîye. The cassava plant grown from spontaneous seedlings. New varieties are often acquired through the incorporation of volunteer cassava plants grown from seedlings, the products of sexual reproduction, that appear spontaneously in farms (Makushi Research Unit 1996). Although cassava has long been propagated vegetatively, it has retained its ancestral capacity for sexual reproduction. In Makushi farms, most varieties produce flowers, and these produce fruit which dehisce at maturity, dispersing their seeds before the plants are harvested. Seeds are projected on the ground by exploding capsules, and then secondarily dispersed by ants (Elias and McKey in press) and perhaps by other mechanisms. Although seed physiology is poorly documented, variable dormancy has been reported (N. Morante, Centre Internacional de Agricultura Tropical, Cali, Colombia, personal communication), and scattered anecdotal observations seem to show that preserving a vegetation cover prevents seed germination.

Seeds germinate whenever a new farm is cut in an old fallow. Spontaneous seedlings, ***tepuru pîye*** (from ***tepuru***, seed) are found in places that were cultivated as long as 35 years ago. One farmer even found a ***tepuru pîye*** plant in a farm he had just cleared in a high forest location three hours down river by canoe from Rewa, which was, according to oral tradition, last cultivated by a group of Caribs more than fifty years ago. He decided to multiply it, and called the new variety ***kari'na pîye***, "Carib stick." The surprisingly long dormancy suggested by this observation and by Amuesha comments (Salick et al. 1997) can be explained by the presence of seed banks along with seed propensity for long survival (Elias and McKey in press). Dormancy of seeds from a seed bank must be broken by cues. Many light-demanding tropical pioneer species respond to changes in light quality or soil temperature regimes following removal of vegetation. In others, germination is enhanced by the direct (high temperature) or indirect (higher concentration of minerals in ash) consequences of fire (Garwood 1989). Some of the cues that break dormancy of wild *Manihot* species and cassava seeds have been identified; they involve high temperature (Ellis et al. 1982; Nassar and Teixeira

1983) and scarification. As seedlings usually start growing before the first cuttings are planted, they do not suffer much competition from planted cassava. We have yet to gather information on the survival rate of seedlings. Up to 400 seedlings have been found in one young crop of 425 m_ (Elias and McKey in press), which is the highest density ever reported in the literature (Emperaire et al. 1998 report one or two seedlings per farm).

Farmers pay special attention to plants grown from spontaneous seedlings, which they have no difficulty identifying. Although they may compete with, and affect the growth of, planted cuttings, seedlings are only rarely weeded, and usually left to grow until they reach maturity. Like common varieties, they are harvested and their roots processed. If the farmer is satisfied with the yield, the color of the root, and any other characteristic, the stem is divided into cuttings which are soon replanted and multiplied in a specific location. If the tuberous roots are found unsatisfactory, the stem is generally discarded, although farmers keen to experiment clone it, hoping that it will become more productive after one cultivation cycle. ***Tepuru pîye*** are thus multiplied over generations of planting, and, since they often present novel combinations of morphological characters, are usually treated as new varieties. Naming these new phenotypes is not easy. Audacious farmers create appropriate names, such as, for example, Mr Nathaniel Edwards in Rewa, who, without hesitation, named a "very yellow" variety from a spontaneous seedling "I love stick" (***waakîri pîye***). Most farmers, however, take the view that all varieties are pre-existent, each with a fixed name, and so prefer not to invent new names. Consequently, they keep the non-specific denomination ***tepuru pîye***, which they apply to different phenotypes.

When the characteristics of a seedling closely match those of a known variety, the seedling, assumed to have grown from the seed of this particular variety, is assimilated to, and named after it (adding the term ***perurupe***, such as in ***paranakîrî pîye perurupe***, "seed of white man stick"). Seedlings which are considered entirely identical to a known variety are treated exactly like any other member of this variety. In the field, we were able to document four cases of such pseudo-reappearance of a known variety from a seedling. However, we suspect the frequency of complete assimilation of seedlings to known varieties to be much higher. Whereas it is easy to put one cutting aside in order to multiply a given variety, this is not the case when a great number of cuttings from the same variety have to be distinguished, hence the unconscious confusion and unintentional mixing of cuttings originating from seedlings with cuttings from pre-existing varieties. Farmers may not remember the seedling origin of particular stems, if the morphological characteristics of the latter are not sufficiently distinctive. Some of the farmers we interviewed were actually aware of making mistakes when identifying varieties, and of accidentally including new seedling phenotypes within known varieties. The assimilation of plants from seedlings into known varieties is one of the reasons for intravarietal genetic diversity in cassava grown by the Makushi (Elias et al in press), which is associated with intravarietal phenotypic diversity. Adding to the frequency of such confusion between similar varieties is the fact that the phenotypes of a given variety also vary with environmental factors.

Obtaining quantitative data on the incorporation of sexually produced indi-

viduals into the stock of material for vegetative propagation was extremely difficult. One farmer, a highly respected widow with a level of education above average, told us that in the high-forest farms cultivated by her husband and herself over a period of 15 years, cuttings from seedlings came to represent 30 per cent of the varieties grown, against 15 per cent for the varieties with which they planted the first farm in the area, and 55 per cent for the varieties they acquired through exchange with neighbours and relatives. We do not know whether this case is exceptional or representative. One would expect to find many varieties derived from seedlings in every farm, given the high density of seedlings growing in cassava farms, and the information volunteered by farmers, who say they multiply most of the ***tepuru pîye*** they find in their farms. However, when asked for the varieties previously multiplied from ***tepuru pîye***, farmers only name on average one or two (the maximum was eight). Such a contradiction can be explained by the aforementioned phenomenon of assimilation of ***tepuru pîye*** into other varieties. Another possible explanation is that these varieties, which are represented by a small number of individuals in the first generations, are easily lost. Besides, their identification requires a special memorisation effort on the part of farmers.

Seedlings are not only the sole source of novel genotypes; they are also, at times, the only source of cuttings. In 1950, as reported by many old people, farmers in the savanna experienced a very severe drought, which lasted almost two years. Their crops dried out, and they soon ran out of planting material, which they recovered by clearing old farm locations, where seeds germinated, providing them with new stocks of cuttings.

Local wisdom, according to which cuttings produce individuals similar to those from which they come (i.e. identical genotypes), is contradicted by the behaviour of ***tepuru pîye***, which rarely reproduce the characteristic features of the particular varieties from which the seeds originate, but display instead novel or unusual combinations of traits, due to recombination in a genome that is very heterozygous (Colombo 1997; Lefèvre 1989), a property enhanced by allogamous reproduction (Rogers 1965). Makushi farmers, who find the unusual trait combinations of seedlings quite puzzling, explain them by presuming that a seed from a given variety, because of its small dimensions, is influenced by other varieties after falling to the ground, and denatured.

This perception may in turn explain why they never plant cassava seeds, but propagate clones of ***tepuru pîye***, despite their knowledge of seed planting, a technique commonly used to grow crops such as papaya and corn. It may also explain why farmers never give away cuttings from spontaneous seedlings, but only cuttings from third or fourth generation clones, which they have replanted in various types of soil, and observed. In any case, cuttings from ***tepuru pîye*** are greatly appreciated for their "vitality," their "youth." As one farmer told us, normal cuttings (i.e. clones) get too "accustomed to the soil," they are too "tamed," and end up producing less and less, while cuttings from spontaneous seedlings often produce increasingly better yields (see Rival [in press] for further discussion of cultural representations associated with ***tepuru pîye***).

DISCUSSION

Makushi cassava diversity in the Amazon context.–Bitter cassava is the staple crop of most lowland Amazonian Amerindians, and the Makushi, who possess at least 76 varieties, are no exception. This high varietal diversity is comparable to the diversity encountered in other groups. Grenand (1993) counted 31 bitter varieties in a Wayãpi community in French Guiana, and Carneiro (1983) 46 among the Kuikuru of Brazil; Emperaire et al. (1998) found 61 bitter varieties in one caboclo village, and a total of 140 names among all the villages they studied; Dufour and Wilson (1996) found more than 100 varieties among Tukanoans from Yapu in Colombia, and Chernela (1987) collected 137 different names among four communities along the Uaupés river in Colombia. A comparable level of diversity is encountered among sweet cassava farmers: 117 names were collected by Salick et al. (1997) in 16 Amuesha communities, and more than 100 by Boster (1984b) among the Aguaruna in Peru.

Genetic implications of traditional management.–Despite its peculiarities, the Makushi farming system, which shares many features with other native Amazonian cassava farming systems (slash-and-burn agriculture, strong environmental pressure, conservative human selection, planting system, incorporation of seedlings, and so forth), can be used as a model to study the genetic consequences of traditional management.

Cassava, which grows in an ecosystem shaped by both environmental and cultural factors, is the target of two interacting types of selection, natural and human. Human selection is either conscious or unconscious. Genotypes constitute ultimately the units of selection in both natural and unconscious human selection. In the case of deliberate human selection, however, the units of selection are the taxonomic units. One taxonomic unit can include several genotypes, given the assimilation into a single variety of different clones with similar phenotypes and of plants of sexual origin. If a farmer decides to multiply such a heterogeneous variety, she or he may multiply not only one genotype, but several, while, at the same time, taking the risk of losing other genotypes, because (1) genotypes sharing the same phenotypes are indistinguishable, and (2) no special effort is made to maintain all the intravarietal phenotypic variation (Boster 1985).

Although human and natural selection have distinct origins, they nevertheless act as similar agents of evolution (Salick 1995), and may even interact. Human deliberate selection on features such as productivity can be superimposed on, and reinforce, natural selection. In a given environmental context, selection for productivity can constitute selection for resistance to drought, herbivory, or other ecological factors (Johns 1990; McKey and Beckerman 1993). To understand the observed patterns of varietal diversity, therefore, both natural and artificial selection must be taken into consideration.

What are the consequences of natural and human selection, and of their interaction, on genetic diversity? Pressures may either increase or decrease varietal diversity. At the farm and community level (intervarietal diversity), environmental pressures may lead to local or short-term decreases in varietal diversity. Varieties

can be lost, for example, during a flood or after ant attacks. Human selection may also lead to decreased diversity, when a variety is accidentally lost because of lack of suitable space to plant it, or when it is deliberately discarded. Since criteria for discarding a variety are mainly based on productivity, human selection acts, in this case, in the same direction as natural selection.

Human selection can also increase varietal diversity. Makushi farmers tend to favour new varieties that are more liable to disappear, for they are represented by a few individuals only. Since the environment is highly variable and unpredictable, natural selection will not always favour the same genotypes. Makushi appreciation of diversity for its own sake leads them to keep many varieties, even if they are not currently very productive. Although this is not an explicit, deliberate strategy, the result is possession of a varietal pool globally resistant to many kinds of pressures.

Unlike most tuber crops, cassava is propagated by stem cuttings, a material different from the edible part. The absence of use competition between material for propagation and for food enables farmers to be more selective about what is planted. With exchanges of planting material occurring widely among villagers, a variety accidentally lost in a farm is easily recovered, and the risk of losing varieties greatly diminished within the community. Such exchanges also allow farmers to acquire new varieties and increase their own varietal diversity. Furthermore, exchanges taking place between different communities lead to increased diversity at the village level. Intervarietal diversity is further increased with the multiplication of volunteer plants grown from seedlings, ***tepuru pîye***, which create new genotypes. Aside from somatic mutations, probably of rare occurrence, ***tepuru pîye*** are the only source of original diversity.

Compared to many other Amazonian groups, the social context of Makushi farming is favourable to a high degree of varietal diversity. Firstly, in the Makushi farming system, each household manages varietal diversity on its own farms. In contrast, the Amuesha (Salick et al. 1997) delegate the management of diversity to their shamans, who not only must grow many more varieties than other farmers, but who are also responsible for experimenting with the plants grown from seedlings. Such a centralised system based on a reduced number of specialists may have the advantage of ensuring a more homogeneous redistribution of diversity, but it is far more vulnerable. Secondly, and although they are said to be acculturated, having been converted to Christianity (but see Butt-Colson's [1967] work on Pemong and Akawaio millenarist movements) and having lost many of their customs and traditions, the Makushi have preserved a strong sense of collective identity and have maintained their traditional subsistence agriculture. Makushi choices on whether or not to plant a given variety, and on the frequency of planting each variety, are still personal choices which are not yet dictated by the market economy or any other external factors. Their situation differs from that of detribalised and socially destabilised Tukanoans described by Grenand (1993), who have lost their knowledge of cassava cultivation and processing, a loss that has led to a dramatic impoverishment of cassava diversity in Tukano land. Thirdly, Rewa and other Makushi forest villages are not subjected to market forces. Various authors (Salick et al. 1997; Emperaire et al. 1998) have shown that markets

push farmers to increase productivity and to cultivate a restricted range of commercial varieties, furthering the tendency to grow highly productive varieties at the expense of rarer varieties that may, as a result, get lost.

We have presented the ways in which intervarietal genetic diversity is shaped by environmental and human pressures. But what are the genetic consequences at the intravarietal level? Scientists studying cassava genetic diversity commonly assume that varieties are clonal, because they are propagated vegetatively. However, the incorporation of sexually produced cassava in a variety, and more generally, the confusion between two types of cassava that have similar phenotypes, lead to intravarietal genetic diversity (Colombo 1997, Elias et al. in press). Intravarietal diversity is observed despite the fact that each variety is subject to a phase of intense genetic bottleneck, when cuttings are selected for the next generation. Since an adult plant can provide from two to fifteen cuttings, a farmer often has too many cuttings to plant, except when he or she is planting a new farm. Surplus cuttings may be given to neighbours or relatives who need them, but the bulk is simply planted in large bundles at the edge of the farm. These cuttings are functionally 'dead,' since they will either die out, or grow without being replanted. In other words, only a small proportion of individuals in each variety participates in producing future generations. Some genotypes may be eliminated in this way through genetic drift, leading to a decrease of intravarietal genetic diversity at the farm level. Observed intravarietal diversity (Elias et al. in press) is thus the result of the balance between the frequency of confusion of plants sharing similar morphological characters, and the strength of genetic bottlenecks.

CONCLUSION

The results presented here illustrate the ways in which selective pressure is exercised by various socio-cultural factors. This study should be regarded as a first step in the proposed integrative approach, which will be used as a background for understanding forthcoming results of genetic analyses and ecological experiments.

NOTES

[1] The putative wild relative of cultivated cassava *Manihot esculenta* subsp. *flabellifolia* (Olsen and Schaal 1999) is not found around Rewa, but small populations exist around other villages in the savannah area (at least 75 km away from Rewa). Wild cassava (***kwana***) cuttings are not planted, nor are the tuberous roots used, although old people in the savanna report having eaten mixtures of wild cassava and cultivated cassava roots during times of starvation in the 1950s. Genetic data (Elias et al., in press) suggest that gene flow from wild cassava is not a significant evolutionary factor in cultivated populations in Guyana, and that the local wild gene pool has contributed little to the diversity of the cultivated pool.

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